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**Kleptoparasitism in gulls (*Laridae*) at an urban and a coastal foraging  
environment: An assessment of ecological predictors.**

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## ABSTRACT

**Capsule:** Kleptoparasitism in gulls occurred at a greater rate at an urban compared with a coastal site. Population density and prey size predicted the rate of kleptoparasitism at the urban site.

**Aims:** To investigate and assess the ecological variables associated with kleptoparasitism among gulls at urban and rural sites.

**Methods:** Field observations were conducted at Brancaster (coastal rural) and Billingsgate Market (urban) to examine differences in the rate of kleptoparasitism in mixed-species flocks of gulls. Four key variables (prey size, population density, season and species) were assessed as predictors of kleptoparasitism.

**Results:** Generalized linear models revealed significant effects on kleptoparasitism rate of site, population density and prey size, and two-way interactions between these main terms. Population density and prey size differed significantly between sites, but population density appeared to predict the rate of kleptoparasitism.

**Conclusion:** Kleptoparasitism may well aid invasion and increase the range of environments a gull can tolerate by helping them meet their energy needs in novel environments where normal foraging behaviours are difficult to implement.

## INTRODUCTION

Kleptoparasitism can be defined most simply as “seizing food gathered by another” (Hatch 1970) and it is a foraging strategy that can reduce the costs of searching for and procurement of food (Thompson 1986, Barnard 1990, Giraldeau & Caraco 2000, Giraldeau & Dubois 2008). Kleptoparasitism has been observed within and between species across various animal taxa (Brockmann & Barnard 1979) including insects (Erlandsson 1988), spiders (Coyle *et al.* 1991), mammals (Höner *et al.* 2002), and even humans (Schoe *et al.* 2009). Birds, more than other taxa, have been the focus of detailed research in this area (Barnard 1990). In a seminal and exhaustive review of the avian literature, Brockmann & Barnard (1979) identified gulls *Laridae* as the most prevalent kleptoparasites and listed ecological factors conducive to kleptoparasitism. These included large concentrations of hosts (victims) and quantities of food, and large, high quality food items to steal. Here, we focus on kleptoparasitism within and between gull species in two distinct ecologies.

Research on gulls has demonstrated that kleptoparasitism is a facultative behavioural strategy that is applied flexibly as ecological conditions vary. Field research conducted by Maniscalco & Ostrand (1997) found that the degree of kleptoparasitism covaries with the concentration of hosts. In mixed-species foraging flocks of seabirds the rate of kleptoparasitism committed by gulls increased as the density of birds increased. The distribution of food resources covaried with foraging flock density, such that food distribution should directly predict rates of kleptoparasitism.

Hamilton (2002) explored the relationship between food availability and kleptoparasitism by assessing the distribution of foragers between patches that were high or low in the rate of food input. The model showed that less kleptoparasitism occurred in high resource input patches and that kleptoparasitism increased with decreasing resource input. Increasing the density of competitors in a patch had the effect of increasing the proportion of kleptoparasites, in line with the observations of Maniscalco & Ostrand (1997). Increasing the number of competitors and decreasing resources increased the intensity of resource competition, thus promoting kleptoparasitism.

The findings of Maniscalco & Ostrand (1997) and Hamilton (2002) strongly indicate that kleptoparasitism is a flexible behavioural strategy. However, no research has yet investigated the value of kleptoparasitism in evolutionarily novel environments. The increasing urbanisation of gull populations provides an opportunity to address this question. Many gull species that are found in urban settings are of conservation concern due to declining populations over the last 25 years or more (Eaton *et al.* 2015).

Understanding the behavioural strategies adopted by these species will help to further understand the stresses they face (Eaton *et al.* 2015, Reid 2004, Madden & Newton 2004).

Gulls are found in a variety of habitats (Pons *et al.* 2005) and have been noted for their tendency to colonise novel environments (Rock 2005). As members of the sub-order *Charadrii* they are part of only two groups of modern birds known to have been present since the Cretaceous period over 65 million years ago (Proctor & Lynch 1993). Their significant investment in kleptoparasitism highlights the importance of this strategy to gull species, and suggests kleptoparasitic behaviours may have played an important role in aiding the radiation and longevity of this family. For any animal, invading an urban environment entails finding solutions to a number of survival problems, the most pressing of which is acquiring food. Kleptoparasitism is a foraging strategy that can be used by gulls when very few conditions are met. The only essential conditions are the availability of opportunistic food sources and the presence of other foragers, of any species, to provide cues as to the location of food.

In this study, we investigated the predictors of the rate of kleptoparasitism in foraging gull populations across two environments with contrasting parameters: 1) a coastal environment, assumed to be typical of the shoreline foraging ecologies encountered by gulls throughout much of their evolutionary history and 2) an urban environment. Our predictions were: 1) that population density would be positively related to the rate of kleptoparasitism, 2) that large prey items would be more susceptible to theft, so that prey size should covary with kleptoparasitism rate, 3) that kleptoparasitism would vary between breeding (March to August) and non-breeding seasons, 4) that gull species would differ in their use of kleptoparasitic behaviour and 5) that there would be a higher rate of kleptoparasitism at the urban site, where food was predicted to be a rapidly decreasing resource.

## METHODS

### Study Sites

Research was conducted at two sites in the UK, between July 2014 and June 2015. Three days of observations were conducted at each site in all calendar months. Site 1 was Brancaster Beach, Norfolk, UK (52°58'30"N 0°38'11"E); a public beach situated within a saltmarsh environment, managed by the National Trust. The low tide at Brancaster exposes a large area of sand beach where numerous bird species forage for prey items exposed by the receding tide. The study area was a section of beach demarcated by two water channels where the outflow of water draining from the saltmarsh joins the sea. These two channels marked the eastern and western boundaries of the study area. At its maximum, when the tide was at its lowest point, the study area covered 1.6 km<sup>2</sup>. Site 2 was an urban location at Billingsgate Market, east London (51°30'20"N 0°00'43"W); a commercial fish market. Research was conducted in a car park used by fish merchants to process and load stock onto vans, and covered an area of 0.0104 km<sup>2</sup>. The size of study areas was calculated using scaled aerial photographs from Google Maps.

### Study species

Large numbers of gulls aggregated daily to forage at both sites. At Brancaster, gulls aggregated to forage in mixed-species groups over a period of about four hours; two hours either side of the low tide mark. The most numerous gull species present at this site were Great Black-backed Gull *Larus marinus*, Herring Gull *Larus argentatus*, Black-headed Gull *Chroicocephalus ridibundus* and Common Gull *Larus canus*. These four species were the focus of research at Brancaster throughout the year. However, the numbers of Common Gulls and Black-headed Gulls were lower during the summer months as birds were mostly away breeding elsewhere. The foraging population of gulls at Brancaster had a mean daily population size of 176 (Range: 0 - 924) gulls. The daily mean number (and % of population) of each species at the site was: Herring Gull 75 (42%), Black-headed Gull 64 (37%), Common Gull 31 (18%) and Great Black-backed Gull 6 (3%).

Gulls aggregated at Billingsgate to exploit seafood waste and food leftovers discarded in the car park areas. The population consisted of Great Black-backed, Herring and Black-headed Gulls, and all three species were the focus of research. Great Black-backed and Herring Gulls were present at Billingsgate all year round, with some birds nesting on the surrounding market buildings. Black-headed Gulls were largely absent from the site between the April and July when they were away breeding elsewhere. The

foraging population at Billingsgate had a mean daily population size of 40 (Range: 24 - 79) gulls. The daily mean number (and % of population) of each species at Billingsgate was: Herring Gull 28 (70%), Black-headed Gull 7 (19%) and Great Black-backed Gull 4 (11%).

### **Measuring kleptoparasitism**

Population size and composition were calculated using scan samples at 30 minute intervals. All attempts at kleptoparasitism, both successful and unsuccessful, were counted. Kleptoparasitic behaviours included the use of force to take items from another bird, theft without any interaction with the host and simultaneous theft (or attempted theft) from a host, by two or more competitors (Giraldeau & Caraco 2000). Size of food items was estimated visually in relation to bill lengths. The Herring Gull bill length was used as a standard comparative measurement to assess the length of food items (Table 1). Food items contested by the smaller or larger species of gulls were calibrated in relation to the mean size of Herring Gull bills. Prey sizes were assigned to increasingly large categories in relation to Herring Gull bill size (0.5, 0.75, 1, 2, 3, 4, 5 or 6).

[INSERT TABLE 1 ABOUT HERE]

### **Field observations**

*Brancaster:* The majority of field sessions were conducted at low tide to coincide with the presence of the largest numbers of birds. Field sessions had a mean duration of 120 minutes (range: 90 – 220 minutes) and a total of 74 hours 28 minutes of observations were conducted at Brancaster over 34 days. Field sessions were conducted during daylight between 04:45 hours and 17:00 hours, to permit behaviour to be recorded on video.

An observer (RS) scanned the beach for gulls, using binoculars, and then approaching to within a distance from which foraging patches could be identified, the gulls counted and their foraging behaviour recorded on video. Patches were classified as discrete clusters of two or more birds exploiting a food source or searching for food in a given area. The location of patches was constantly shifting around the beach. Once a patch was identified, video recording was carried out from a fixed position with a Sony 8.9 megapixel HD camcorder mounted on a tripod. The distance from which a patch was filmed varied and was contingent on how closely the researcher could approach without

disrupting the foraging birds. Recording of a patch was concluded when the gulls in that patch dispersed. The duration of recordings ranged from 32 seconds to 40 minutes 47 seconds, and 142 patches were recorded in total. Videos were analysed at a later date for incidents of kleptoparasitism.

Gull counts were conducted every 30 minutes from the start of a field session, using a series of digital images (Nikon Coolpix P510 42x zoom) taken to record all gulls in the study area. These images were analysed at a later date to calculate the population size and composition.

*Billingsgate:* Observations at Billingsgate were conducted between 07:00 hours and 15:00 hours. The trading hours for the market were 03:00 hours to 08:30 hours. After 08:30 hours, the main activity at the site is the clean-up of the market and car park. Prior to 07:00 hours it was not possible to conduct observations due to the large number of vehicles at the site. Field sessions were conducted on days when the market was operational (Tuesday to Saturday) and when it was closed (Sunday and Monday).

Observations and recordings were conducted from a vehicle placed to give the best vantage point on the day and the position varied between observation days. Gull activity at foraging patches was video recorded by the observer (RS) until the resource in the patch had depleted and the birds dispersed. Over the study, 183 foraging patches were recorded and these ranged in duration from 25 seconds to 29 minutes 36 seconds. For each recording we noted the number of each species and ages of the gulls present. Patch videos were analysed at a later date for incidents of kleptoparasitism.

Gull counts were conducted at 30 minute intervals from the start of a field session. As at Brancaster, a series of digital images were taken of the study area, and later analysed to calculate the population at the time of the sample, including the species and ages of gulls present. The same recording and photographic equipment used at Brancaster was used at Billingsgate.

## **Statistical analysis**

All statistical analyses were conducted using R version 3.3.1 (R Core Team, 2016). Figures were produced in R using the base package or ggplot2 version 2.1.0 (Wickham, 2009).



## RESULTS

In total, there were 595 kleptoparasitic events recorded at Billingsgate and 99 at Brancaster. A single event involving a Lesser Black-backed Gull *Larus fuscus* was excluded from the analysis. There were 15 missing data points for prey size and all data associated with these observations were also removed.

Data were analysed using a series of generalized linear models (GLM). The response variable was the rate of kleptoparasitism (events per minute) for each patch observed. This variable was  $\log_n$  transformed to improve the dispersion of data. The predictor variables were population density (daily mean population density (birds.km<sup>-2</sup>) over each study area), prey size, season (breeding/non-breeding), species of kleptoparasite and site (Billingsgate/Brancaster). The population density, prey size and response variables were each centred and scaled in order to standardize them. Standardizing continuous variables facilitated meaningful comparisons between model coefficients. All variables were entered as main effects into a GLM using a Gaussian function with identity link (Table 2).

To avoid over-fitting a relatively small dataset, we next adopted a subtractive approach using a backward `step()` function. This is a sequential approach to model fitting using the Akaike Information Criterion corrected for finite sample sizes (AICc). Models with AICc values which differ by less than 2 are regarded as being similarly good fits, whereas differences ( $\Delta\text{AICc}$ ) over 2 suggest the model with the higher AICc is a poorer fit (Burnham & Anderson 2001). This approach led to the removal of season and species from the best fitting model, leaving a minimal main effects model with site, standardized population density and standardized prey size as significant predictors of kleptoparasitism rate (Table 2).

[INSERT FIGURES 1 & 2 AND TABLE 2 ABOUT HERE]

A positive correlation was apparent between population density and standardized  $\log_n$  kleptoparasitism rate at Billingsgate, and to a lesser extent at Brancaster (Figure 1). A positive correlation was also seen between prey size and standardized  $\log_n$  kleptoparasitism rate at Billingsgate, but this correlation appears to be negative at Brancaster (Figure 2).

Owing to the trend differences noted between sites (Figures 1 and 2), a second (Gaussian) GLM was constructed which included the main effects and all pairwise

interactions between site, standardized prey size and standardized population density. This model suggested that the interactions were significant (Table 2). Notably, however, the coefficients for the main effects of site, standardized prey size and standardized population density remained approximately the same (Table 2) indicating that the data collected at Brancaster did not evidence a trend reversal.

Data from Brancaster showed a smaller range of values for prey size and population density than Billingsgate, and in the case of population density the data ranges for the two sites were non-overlapping (x axes in Figures 1 and 2, Table 3). This suggests that additional data may be needed to be collected at Brancaster (or an equivalent site) to capture the influence of these variables on kleptoparasitism across this reduced ranges. Prey sizes and population densities were both significantly greater at Billingsgate (Table 3).

[INSERT TABLE 3 ABOUT HERE]

Returning to the response variable and to explore the relative importance of pairwise interactions in the interactions model we again adopted a subtractive  $\Delta\text{AICc}$  approach (using the `drop1()` function). All three pairwise interactions between the three entered variables could be removed while lowering the AICc with one exception: the site  $\times$  prey size interaction. Removing only this interaction from the model resulted in an increased AICc. The reasonable fit offered by models of kleptoparasitism that include interactions and the significant differences between the two key continuous predictor variables support the view that the two sites show a core ecological difference.

## DISCUSSION

Our results show that rates of kleptoparasitism in gulls are affected by bird population density and prey size. While these two predictors seem to be robustly positively correlated with increased rates of kleptoparasitism, differences between the sites in the predictors and the response variable support a more cautious interpretation. It is possible that the population density measure may under-estimate the search time entailed for would-be kleptoparasites at Brancaster, in contrast to Billingsgate.

Maniscalco & Ostrand (1997) demonstrated how a shift in the foraging conditions in a single environment resulted in an increase in kleptoparasitic behaviour by gulls. Our results complement that finding and describe clear frequency differences between a rural and an urban site. Our study gave focus to the role that kleptoparasitism might play in helping gulls meet their energy needs when invading urban environments. Our sample size is small – one rural and one urban environment only – and so we must be cautious in generalizing any findings. However, here we consider the mechanism by which urban invasion might occur when birds initially encounter those spaces. As Marzluff *et al.* (2001) have described, the foraging environment changes on a gradient between wildland environments and heavily urbanised spaces. As a gull moves along this gradient it will encounter fewer aspects of the foraging environment with which it is familiar. At one extreme of this gradient are heavily urbanised spaces containing lots of anthropogenic novelty with few of the characteristics of a natural food web. Billingsgate is such a site, as all the food there is waste provisioned by human activities. A gull, or small founder population of gulls, invading an urban environment must either obtain food through: innovation by exploring the novel foraging space; learning what things are edible and where to find them by copying other foragers; or stealing food from other individuals.

Previous research has emphasised the importance of innovative behaviour in species that invade novel environments (Sol *et al.* 2005, Sol *et al.* 2008). Some proportion of innovators, who explore the environment, are essential in any population otherwise there would be no one to copy, however, rates of innovation in any natural population are quite low (Page 2008), making the second two options, copying or stealing, more likely for invasive gulls. Of these, copying other foragers to learn the locations of food is necessary, but stealing can be efficient as it avoids the cost of the full foraging cycle by acquiring food discovered by another's effort. To this end, we can think of stealing information and stealing food as on a continuum; the cost of stealing the food is actually the marginal cost of stealing conditional on already observing the victim.

As gulls can range over large areas they can occupy different habitats on the gradient described above in a single foraging bout or day. This suggests a plausible

alternative mechanism to the one described above by which gulls can invade urban spaces. They can forage in environments where they encounter conditions with which they are familiar, and then make forays and encroachments into urban spaces in search of supplemental food and other foraging populations. Foraging in the littoral zone of rivers and estuaries that pass near or through cities is an example of how this might work. In our argument regarding the utility of kleptoparasitism we have made the assumption that while this second mechanism would undoubtedly occur, the additional travel and foraging costs involved would make it energetically more expensive than exploiting other foragers through kleptoparasitism. These costs would not be prohibitive of this foraging approach but we suggest that these additional costs would make it secondary to the kleptoparasitic strategies considered above. At present little is known about the foraging habits and ranges of urban gull populations, and tracking of individuals to see the extent of their foraging ranges was not undertaken in our study. Further work of this nature would be useful to assess whether urban gull populations, such as the one at Billingsgate, obtain their food exclusively at that site or exploit a variety of habitats.

Comparing the range and diversity of environments occupied by different gull species may also provide insights into the role of kleptoparasitism in supporting invasion. As described by Brockmann & Barnard (1979) 23 of 88 gull species are reported to use kleptoparasitism. A comparison between kleptoparasitic and non-kleptoparasitic gull species of the diversity of habitats that these species routinely breed and forage in, and the extent of their ranges, may provide indirect evidence for the proposed role of kleptoparasitism as a strategy that buffers against environmental change. If this proposed function of kleptoparasitism is plausible we should expect to see kleptoparasitic gull species occupying a broader diversity of habitats than non-kleptoparasitic gull species.

#### *Ecological predictors of kleptoparasitism*

Birds are dispersed widely at Brancaster and population density was positively correlated with kleptoparasitism. This finding is consistent with empirical research that shows foragers are more likely to encounter each other at high population densities and interact aggressively (Colwell 2010). It also lends support to the theoretical model of Hamilton (2002) demonstrating increased kleptoparasitism with increasing competitor density.

In addition, King *et al.* (2009), in research on baboon troops, found that the distribution of resources influenced the rate of kleptoparasitism, with small tightly

clustered patches prompting more kleptoparasitism. The resources in the study environments at Brancaster and Billingsgate were clearly distributed in different ways that provided a useful test of the pattern of behaviour described by King *et al.* (2009). The food at Brancaster was naturally more widely dispersed throughout the environment and it was a much larger study area than Billingsgate, permitting gulls to be more spaced out whilst foraging. Our results support the finding of King *et al.* (2009) with more kleptoparasitism in high density areas where gulls were forced to forage closer together, perhaps making it easier to take advantage of opportunities to try and steal.

The finding that larger food items were more likely to be targeted for theft is in accord with the findings of several empirical studies (Hopkins & Wiley 1972, Ens & Cayford 1996, Leeman *et al.* 2001). Large prey items provide a conspicuous visual cue to the presence of food, and a large prey item requires longer handling time, which increases the likelihood that other foragers can approach and try to steal the item. Our use of an ordinal scale to measure the size of prey items in terms of bill lengths was a limitation of this study that may have resulted in a loss of additional data of value. Ordinal measures of this kind result in a lack of precision that may mask useful patterns of behaviour. A more finely grained measure would have been beneficial, but the ordinal measure of bill lengths used represented the most practical way to assess the size of food items from the observational data obtained.

*Concluding remarks:* Kleptoparasitism was higher in the urban environment. Large prey items that take longer to handle, and high population densities that increase competition for available resources were the critical aspects of the urban environment at Billingsgate that promoted kleptoparasitism. Kleptoparasitism may well aid invasion and increase the range of environments a gull can tolerate by helping them meet their energy needs in novel environments where normal foraging behaviours are difficult to implement.

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## Tables

**Table 1.** Data used to obtain a standardised bill length measurement. Calculated by taking the mean bill length for both sexes for each species (from Malling Olsen & Larsson 2003), and then taking the mean of all four species' means. This averaging across species returned a figure of 45mm. This was closest to the bill length of Herring Gull (difference of 7mm). The Herring Gull bill length was therefore used to assess the size of food items in the field.

s	m	bill	bill	species bill	s
	length (mm)	length (mm)	length (mm)	length (mm)	bill length (mm)
<b>Common Gull</b>	36.10	32.70	34.40		11
<b>Black-headed Gull</b>	33.60	31.60	32.60		12
<b>Herring Gull</b>	55.20	49.70	52.45		-7
<b>Great Black-backed Gull</b>	63.10	57.60	60.35		-15

**Table 2.** Summary of generalised linear models exploring the effects on  $\log_n$  kleptoparasitism rate (events per minute) of site (with Billingsgate as reference), standardised population density, standardised prey size, species of kleptoparasite and season.

Model	terms	coefficients	AICc	$\Delta$ AICc
a. Main effects model	all		1474.182	6.687
b. Minimal main effects model	site	−0.86128	1468.817	1.322
	population density	+0.45983		
	prey size	+0.08091		
c. Interactions model (two-way interactions)	site	−1.35673	1467.495	0
	population density	+0.43881		
	prey size	+0.08240		

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451 **Table 3.** Differences in prey size and population density between Billingsgate (N = 593) and Brancaster (N =  
 452 86). Differences between site were tested using Mann-Whitney tests.

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Site	median	range	statistic
a) Population density (birds.km <sup>-2</sup> )			
Billingsgate	1.730	0.380 - 4.330	U = 50998, <i>P</i> < 0.0001
Brancaster	0.0190	0.0025 - 0.1250	
b) Prey size (bill lengths)			
Billingsgate	8.00	0.75 - 20.00	U = 46575, <i>P</i> < 0.0001
Brancaster	0.75	0.50 - 6.00	

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457 **Figure Legends**

458 **Figure 1.** Population density plotted against standardized  $\log_n$  kleptoparasitism rate at both sites, with fitted  
459 regression line and shading indicating 95% confidence intervals.

460 **Figure 2.** Prey size plotted against standardized  $\log_n$  kleptoparasitism rate at both sites, with fitted regression  
461 line and shading indicating 95% confidence intervals.

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